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A geometric morphometric analysis of heterochrony in the cranium of chimpanzees and bonobos

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Abstract

Despite several decades of research, there remains a lack of consensus on the extent to which bonobos are paedomorphic (juvenilized) chimpanzees in terms of cranial morphology. This study reexamines the issue by comparing the ontogeny of cranial shape in cross-sectional samples of bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*) using both internal and external 3D landmarks digitized from CT scans. Geometric morphometric methods were used to quantify shape and size; dental-maturation criteria were used to estimate relative dental age. Heterochrony was evaluated using combined size-shape (allometry) and shape-age relationships for the entire cranium, the face, and the braincase. These analyses indicate that the bonobo skull is paedomorphic relative to the chimpanzee for the first principal component of size-related shape variation, most likely via a mechanism of postformation (paedomorphosis due to initial shape underdevelopment). However, the results also indicate that not all aspects of shape differences between the two species, particularly in the face, can be attributed to heterochronic transformation and that additional developmental differences must also have occurred during their evolution.

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Introduction

This study uses geometric morphometric (GM) methods to consider the extent to which the skull of the bonobo (*Pan paniscus*) is paedomorphic (juvenilized) compared to that of the chimpanzee (*Pan troglodytes*). A second, related goal is to test for any dissociation of heterochronies in the skull between facial and neurocranial regions in these two species. Applying heterochrony models to analyze differences between the bonobo and chimpanzee has not only been the subject of much

previous research but also a major test case for theoretical debates concerning heterochrony theory (Shea, 1983a; 1984, 1992; Godfrey and Sutherland, 1996; Alba, 2002; Cobb and O'Higgins, 2004; Mitteroecker et al., 2004, 2005; Ponce de León and Zollikofer, 2006). Yet, despite this attention, bonobo and chimpanzee skulls differ morphologically in ways that have yet to be completely described or understood in terms of their developmental causes and evolutionary implications. While some authors (e.g., Shea, 1992) support the hypothesis that bonobos are paedomorphic relative to chimpanzees, others do not completely support this heterochronic diagnosis for several reasons. Godfrey and Sutherland (1996) used a multivariate allometric model to suggest that the bonobo cranium cannot be described as either paedomorphic or peramorphic relative to chimpanzees because of nonuniform allometries

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between the two species (see below). Additional studies by Williams et al. (2002), Mitteroecker et al. (2005), and Ponce de León and Zollikofer (2006) found that allometric scaling and multivariate analyses can explain only partially the differences between bonobo and chimpanzee crania. Mitteroecker et al. (2004, 2005), moreover, have raised questions about the utility of multivariate analyses such as GM to infer heterochronic transformations.

Here, we expand in several ways upon these earlier studies by using a landmark-based GM approach to compare ontogenetic changes in cranial shape and size between bonobos and chimpanzees using both external and internal landmarks, many of which represent key sites of craniofacial growth. We also use approximate estimates of age based on dental stages in the two species, and we examine multivariate size-shape and age-shape relationships throughout the cranium as a whole and within various regions. Given the potentially confusing nature of research on heterochrony, particularly in light of different methods and terminologies, we begin with a brief review of the GM heterochronic transformation model used here. We then review previous research on whether the bonobo skull is paedomorphic relative to the chimpanzee skull, and outline the hypotheses to be tested and the methods we employ.

Heterochrony model

Ever since Gould (1977), there has been considerable interest in heterochrony, the analysis of changes in the timing and/or rate of developmental events among ancestor and descendant individuals or taxa. Traditionally, heterochronic processes are quantified with respect to three parameters: *shape*, *size*, and *time*. Size and shape describe the *form* of an organism, with size representing a scalar measure of the magnitude of form, and shape referring to aspects of form independent of scale (O'Higgins, 2000). Time can be quantified in several ways, typically as absolute age (chronological time relative to a homologous event such as birth), or in relative terms using a series of stages or events during ontogeny such as tooth eruptions (de Beer, 1958; Smith, 2001).

Implementation of the basic parameters of heterochronic transformation has varied considerably among studies, sometimes leading to alternative methodologies and terminologies (e.g., Gould, 1977; Alberch et al., 1979; McKinney and McNamara, 1991). A major source of confusion and debate has been the issue of time, for which reliable data are often unavailable in many samples. In the absence of good data on the ages of individuals in a sample, researchers typically use size as a proxy to compare size-shape relationships between ontogenetic samples of two or more taxa, effectively converting the analysis to a comparative ontogenetic allometry (Gould, 1977; Fleagle, 1985; McKinney and McNamara, 1991; Godfrey and Sutherland, 1996). Heterochrony and allometry provide complementary but not necessarily equivalent analytic frameworks for analyzing the evolution of ontogenetic trajectories (Klingenberg, 1998). Allometry tests for size-related shape changes; it cannot test directly for temporal differences in development, such as changes in rate and time of offset.

Although there exists a general covariance between size and ontogenetic time, the correspondence between allometry and heterochrony can be complex, making it difficult to infer heterochronic transformation from allometry. Alternative (and often confusing) terminologies have stemmed from multiple models that apply the same terms to heterochronic and allometric plots, which use different parameters to define the ontogenetic changes they portray. Allometry nonetheless sheds light on heterochronic transformations between two species when there is a strong covariance between size and age because heterochronic processes can create various patterns of scaling (McKinney and McNamara 1991; Godfrey and Sutherland, 1995a, b; Godfrey et al., 1998; Leigh et al., 2003).

Allometry, the relationship between size and shape, is used here explicitly as part of our analysis of heterochronic transformation. Changes in allometric trajectories indicate heterochronic transformation, but reflect only indirectly the effects of ontogenetic time (McKinney and McNamara 1991; Godfrey and Sutherland, 1995a, b; Klingenberg 1998; Smith, 2001; Leigh et al., 2003). The evolution of both allometric growth trajectories and aspects of developmental timing are therefore crucial for the understanding of heterochronic transformations because changes in the relationship between size and shape may be independent of that between shape and ontogenetic development.

Size and shape have also been treated in multiple ways. Until recently, most heterochrony studies assessed size using linear measurements, mass, areas, volumes, or occasionally the first principal component of variation of a set of linear measurements (for review, see Alba, 2002). Shape, a dimensionless parameter, has most often been quantified using ratios of two linear measurements. One problem with these measures of size and shape is the issue of size-shape covariation. Lengths, areas, and volumes are not always independent of shape, and the first principal component of multivariate analyses that are not computed from size-corrected data typically includes some component of size-related shape change (Jungers et al., 1995; Mitteroecker et al., 2004).

Geometric morphometric methods that use landmark data are a useful way to measure shape in heterochrony analyses because they can effectively quantify size and 3D shape independently (Zelditch et al., 1995; Penin et al., 2002; Berge and Penin 2004; Cobb and O'Higgins, 2004; Zollikofer and Ponce de León, 2004; Mitteroecker et al., 2004, 2005). Geometric morphometric methods first quantify the form (size and shape) of each specimen according to the location in space of a set of anatomical landmarks that are homologous among individuals. Shape and size are then separated using a Procrustes superimposition of landmarks, which translates the landmarks to a common origin, scales them to a common size, and rotates them to minimize their summed squared landmark distances (Rohlf and Slice, 1990; Zelditch et al., 2004). Procrustes superimposition thus enables one to quantify shape as the multidimensional deviation of a specimen's landmarks from a reference configuration, typically an average of the entire sample. Shape covariation is then quantified using principal components analysis (PCA), a dimension reduction technique

that rotates the landmark configurations (using their covariance matrix) in multidimensional space to identify independent (uncorrelated) linear combinations of geometric landmark shifts (warps) (for discussion, see O'Higgins, 2000; Frost et al., 2003; Zelditch et al., 2004). Plotting the principal component (e.g., PC1 vs. PC2) scores of each individual therefore illustrates aspects of shape differences that covary within a particular *shape space* (O'Higgins, 2000; Eble, 2002). Note that some of the calculated principal components of shape may still be correlated with size, particularly those aspects of shape that covary with ontogeny. Such correlations permit multivariate allometries to be quantified by plotting them versus size. Size can be calculated in a number of ways, including centroid size, the square root of the sum of the squared distances among the landmarks in a configuration and their center of mass (Bookstein, 1991).

Although GM computations of shape present some complications when applied to heterochrony (see Discussion), this study applies GM measures of size and shape to a modification of Alberch et al.'s (1979) model of heterochrony (itself, a formalization of Gould, 1977) to compare the ontogenetic trajectories of the bonobo and chimpanzee. Alberch et al.'s (1979) model allows direct comparison of the dynamics of growth according to the parameters of shape, size, and time. While Alberch et al. (1979) plotted size, shape, and age on three axes, we reduce the inclusive 3D analysis to analyses of allometry (size vs. shape) and heterochronic transformation (age vs. shape) to simplify the depiction and description of ontogenetic differences (Shea, 1983, 1984, 1985). The heterochrony portion plots shape (expressed as principal components of variation among a set of landmarks) against age, allowing one to discern ontogenetic differences in the rate and timing of development by perturbations in initial development, slope, and termination of development (Klingenberg, 1998).

Figure 1 illustrates the diagnostic model employed here (but with several important assumptions that must be considered explicitly) in which differences in ontogeny between closely related species are divided into two categories of endpoint patterns: *paedomorphosis* and *peramorphosis*. In general, paedomorphosis refers to an adult descendant that resembles a juvenile ancestor (an underdeveloped descendant), and peramorphosis refers to an adult descendant that transcends an adult ancestor (an overdeveloped descendant). Paedomorphosis and peramorphosis can be further divided into several categories (representing different heterochronic processes) that are largely discernable using allometry, but which can differ in terms of the relationship between age and shape (Gould, 1977; see also Rice, 1997; Alba, 2002). One key problem to note, however, is that there are multiple trajectories of development that arrive at the same endpoint terminus between age and shape. For example, two species may arrive at the same adult relationship between shape and age, but one species may do so via growth spurts, while the other may have a constant rate of change between the two parameters. Here, for simplicity (and because of the nature of the data we analyze that compares two closely related and similar species) we assume that the regression between age and shape is

linear in both species and varies either in slope or intercept. However, it is important to recognize that there is no reason to assume such linearity, and Fig. 1 does not include many alternative relationships between age and shape that differ in slope and intercept (the reader is encouraged to imagine a variety of nonlinear regressions). These caveats notwithstanding, paedomorphosis can occur according to the simplified model in Fig. 1 via at least five different processes based on the combination of the size-shape allometry and the *end-point termini* of graphs of age vs. shape: (1) *progenesis* (also known as *time hypomorphosis*), in which the descendant prematurely ceases development but size and shape are not dissociated; (2) *neoteny*, in which the descendant has a reduced slope of allometry (size and shape are dissociated) without change in size; (3) *rate hypomorphosis*, in which size-shape relationships remain the same but a reduction in the rate of age-shape development leads to a reduction in size; (4) *postformation*, in which size-shape relationships remain the same but paedomorphosis occurs due to initial shape underdevelopment; and (5) *postdisplacement*, in which size-shape relationships remain the same but paedomorphosis is due to later onset of development. The respective peramorphic equivalents of these are *hypermorphosis*, *acceleration*, *rate hypermorphosis*, *preformation*, and *predisplacement*. Note that it is possible for a descendant to differ from its ancestor by more than one of the above processes.

Despite their advantages, multivariate measures of shape also have some drawbacks and potential complications when used to test hypotheses of heterochronic transformation. For one, the high dimensionality and resulting complexity of shape space can complicate or obscure the interpretation of ontogenies (Klingenberg, 1998; Tissot, 1988). Mitteroecker et al. (2004, 2005) have also pointed out that PCs derived from GM analyses are statistical constructions that combine growth from different regions and thus do not necessarily correspond to actual biological factors. According to their view, heterochronic transformations between two species can only be diagnosed if both “share the same ontogenetic trajectory in multivariate shape space” (Mitteroecker et al., 2005: 256). In other words, two species must have identical shape transformations for multiple PCs to be heterochronic variants. These authors found (using GM methods) that bonobos and chimpanzees share a similar ontogenetic trajectory for just PC1 and PC2, but not PC1 and PC3; hence, they rejected the hypothesis that heterochrony accounts for the differences between bonobos and chimpanzees. A further problem is that principal components analyses can be statistically unstable, so that slight changes to the data set (e.g. landmarks, samples) can change the PCs, resulting in the divergence of the trajectories.

Mitteroecker et al. (2005) raised some important and interesting points, but there are several reasons to reconsider their concerns about the use of individual PCs to test hypotheses of heterochronic transformation in comparisons of very similar taxa such as bonobos and chimpanzees. First, PCs derived from multivariate methods such as GM are no less biologically real as measurements of shape than simpler measurements such as the linear distance between two cranial landmarks

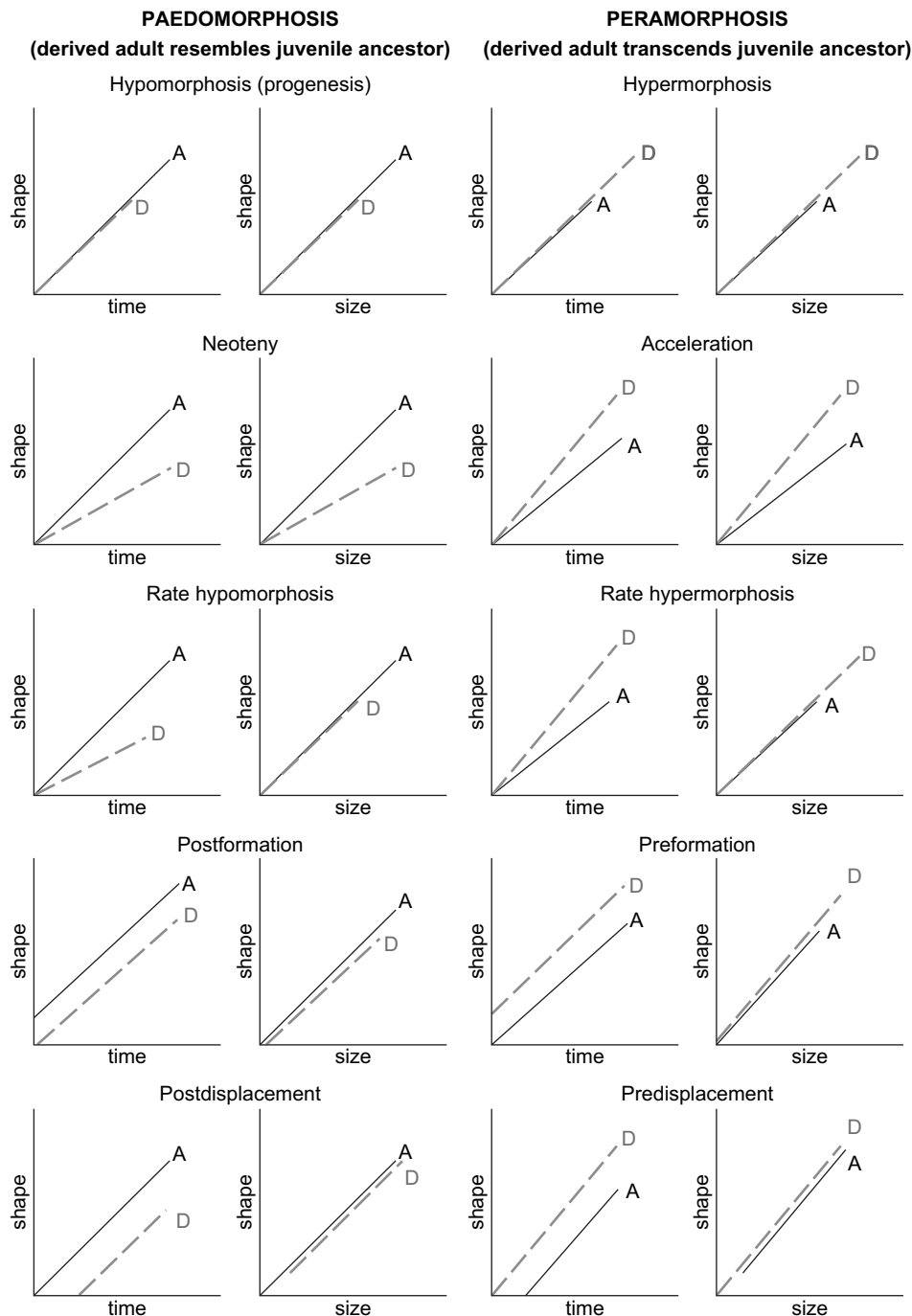


Fig. 1. Simplified heterochrony model used in this analysis (after [Alba, 2002](#)) that combines analyses of relative age vs. shape and size vs. shape. Note that multiple trajectories of development, slopes, and intercepts can produce the same endpoint terminus between age and shape. Here, we plot the slope between age and shape as linear in both species, with variation solely in either slope or intercept. The assumption of linearity, however, is not necessary and a more complete formulation of the model would require many alternative relationships between age and shape that differ in slope and intercept.

(or the ratio of two such measurements). For example, most univariate measurements—such as the chord from bregma to lambda—are integrated consequences of many developmental processes. In the case of bregma–lambda, these processes can include various effects of brain size expansion on sutural growth; many interactions between neural, basicranial, facial, and neurocranial growth processes; the effects of systemic hormones such as growth hormone; and so on ([Weidenreich,](#)

[1941](#); [Moss, 1958](#); [Enlow, 1990](#); [Lieberman, 1996](#); [Lieberman et al., 2000a](#)). Analyses of skulls typically find high degrees of distributed morphological covariation among most measurements because of myriad developmental processes that generate integration within and between regions. Viewed in this light, PCs may actually be better measures of shape than traditional caliper-based measurements because they are statistically independent, and derived without a priori models based

on limited preconceptions about how skulls grow. In addition, PCs can and should be analyzed to derive testable hypotheses about particular developmental processes that generate covariation (Tissot, 1988). Software packages that convert shape spaces into visual models are particularly useful in this regard (for review, see Zelditch et al., 2004). Finally, PC1 by definition accounts for the largest proportion of variation in a data set. In comparing two slightly divergent trajectories among closely related species, it is biologically reasonable to infer that PC1 mostly captures their common direction of ontogeny through shape space, and the variance proportion (eigenvalue) of PC1 indicates their degree of commonality (O'Higgins, 2000). An even more complete, composite description of a common ontogenetic trajectory could be calculated via a multiple regression of all the PCs against size and/or time. The latter method, however, would compute an averaged similarity of transformation, based on multiple independent PCs, and would represent a composite of different, independent transformations. The utility of such a method for testing hypotheses of heterochrony is thus debatable.

A major concern of Mitteroecker et al. (2005) is the diagnosis of heterochrony for species that are not completely scaled variants of each other in multiple PCs (i.e., in some multivariate shape space). Their comparison of bonobos and chimpanzees included only plots of cross-sectional samples for the first three principal components of variation, but they did not plot the relationship of any PC to size or age. They discounted heterochrony as a mechanism of change between bonobos and chimpanzees because the two species had divergent trajectories of shape for PC2 and PC3 (see also Cobb and O'Higgins, 2004). In other words, they found that cross-sectional sample of bonobos and chimps fell along the same trajectory for PC1 and PC2, but differed in terms of PC1 vs. PC3. A conservative way to interpret this divergence is to restrict diagnoses of heterochrony solely to PCs that are parallel in multivariate space, but this criterion is too stringent for several reasons. First, if two taxa had parallel PC trajectories in multiple dimensions, then they would have to be identical in their pattern of shape change, and hence distinguishable using primarily data on age or size. Two different species never exhibit exactly identical morphologies (and are thus identical in multivariate shape space) at different developmental stages. Requiring such colinearity is a sort of all-or-nothing criterion that is not what most biologists, including Gould (1977), have in mind when formulating hypotheses of heterochrony. Evolution is typically mosaic, generating change through heterochronic transformations of components—but not necessarily all aspects—of a descendent organism relative to its ancestor. For example, it is reasonable to hypothesize that the differences between bonobos and chimpanzees could arise through a heterochronic transformation of just facial or neurocranial growth, or through a different transformation of the face relative to the neurocranium. Principal components that show similar ontogenetic trajectories in two closely related species are likely to reflect ancestral patterns of scaling (see Zollikofer and Ponce de León, 2004), but multivariate analyses will almost always identify some PCs with divergent trajectories.

Species such as bonobos and chimpanzees may differ in part from multiple heterochronic transformations, as well as from other kinds of developmental shifts such as heterotopy (evolutionary change in spatial patterning). In this respect, principal components calculated from GM analyses are especially useful because they can help give an idea about what percentage of variation in a sample is accounted for by a particular shared pattern of covariation that scales with size and shape, *and which is statistically independent of other patterns of covariation* (Klingenberg, 1998). Thus, if PC1 scales with size in the same way for two species within the same shape space, then it is not problematic from the perspective of heterochrony *for just PC1* that it may scale differently relative to other independent PCs, because each PC, by definition, quantifies different, independent patterns of shape covariation. That said, one must keep in mind that the percentage of variance explained by a given PC is also a function of nonbiological factors such as sample size, the number and type of landmarks included in the analysis, and so on.

Put differently, PCs calculated from GM analyses are usually graphed as bivariate regressions, so that it is often the case that two species may share the same ontogenetic trajectory (slope and, sometimes, intercept) for PC1 vs. PC2, but not for PC1 vs. PC3 and so on. Under what conditions can it be argued that any of these PCs represents a heterochronic transformation? We argue that if the combined shape space of the analysis is conservative (that is, changing a few variables or specimens does not alter the PCs substantially), and if a given PC (by definition, an independent measure of covariation) scales with size, then one can regress each PC separately against size and time to test hypotheses about allometry and heterochrony. Note that the first condition is more likely to be true for closely related species (such as bonobos and chimpanzees). In addition, the first PC of an analysis will usually correlate strongly with size, but additional information may be contained in other PCs for which correlation with size is not significant.

A final advantage of using GM analyses to analyze heterochrony even when not all PCs scale with allometry is that heterochronic processes can generate complex allometric patterns that may be difficult to interpret solely on the basis of a priori hypothesis testing (Mitteroecker et al., 2004). For example, it is possible that a given heterochronic transformation between an ancestral and descendant species may be regionally localized, such as in the face or in the neurocranium. However, many processes of development can also generate patterns of covariation that scale with size between regions. Such allometries may vary in terms of their pattern of ontogeny, and thus are amenable to heterochronic analysis.

The bonobo hypothesis

Ever since its discovery to science in 1929, the bonobo has been suggested to be a dwarfed version of the common chimpanzee (Schwarz, 1929; Coolidge, 1933), with lower levels of sexual dimorphism in the skull and a smaller overall skull,

particularly the face (Heintz, 1966; Cramer, 1977). The hypothesis that the bonobo is paedomorphic relative to the chimpanzee largely derives from the work of Shea (1983a), whose allometric comparisons showed that the adult bonobo was not simply a dwarfed version of the chimpanzee but instead a mosaic of differently proportioned skull, trunk and forelimb, and hindlimb regions. Since total skull length relative to head–fork length had a lower slope of allometry in the bonobo than the chimpanzee, Shea (1983a) proposed that the bonobo was paedomorphic through the process of neoteny.

As often pointed out (e.g., Godfrey and Sutherland, 1996; Klingenberg, 1998; Alba, 2002), Shea's (1983a) initial analysis had several limitations in relation to the question of whether the bonobo skull is paedomorphic. First, total skull length is not a measurement of skull shape. Second, skull length or other measurements of overall skull shape may confound the existence of multiple, dissociated heterochronic shifts, given the partial modular independence of the face and the complex formed by the basicranium and neurocranium (Moss and Young, 1960; Cheverud, 1982, 1995; Lieberman et al., 2000a, b; Hallgrímsson et al., 2007). Third, Shea's initial analysis included no data on age, which are necessary to diagnose some forms of paedomorphosis. Finally, because both chimpanzee and bonobo skulls scale with negative allometry to body length, the lower slope revealed by Shea's analysis would mean that the bonobo skull is actually peramorphic, despite its smaller size (Godfrey and Sutherland, 1996).¹ This does not mean, however, that bonobos actually have peramorphic skulls because diagnoses of heterochronic growth processes are valid only insofar as they are undertaken *within* a single growth region rather than *between* different growth regions that may scale differently (Alba, 2002).

Since Shea's (1983a) study, others have made further allometric comparisons of bonobo and chimpanzee cranial growth, and these have varied in their methods and findings. These studies differ from that of Shea (1983a) by describing shape as ratios of interlandmark distances and using size measurements that are intrinsic to the skull. When interlandmark distances are compared, mainly using basicranial length and palate length to represent the growth regions of the neurocranium and face, respectively, there is strong evidence for ontogenetic scaling between these measurements (Shea 1983b, 1984, 1985, 1992), implying that the bonobo is paedomorphic through hypomorphosis (or progenesis). When shape is defined as the ratio between basicranial length and palate length, and basicranial length is used as a proxy for size, then the bonobo is reduced in size and juvenilized in shape compared to the chimpanzee at the end of development, but size and shape are not dissociated from each other (Alba, 2002). More in-depth studies (e.g., Shea, 1984, 2000), which compared a larger number of cranial interlandmark distances, found the majority of comparisons to scale ontogenetically (i.e., with the same coefficient of allometry). Interestingly, those few comparisons

revealing dissociated allometries placed the bonobo on the peramorphic side of dissociation from the common allometry: the cranium is wider and the infratemporal fossa and zygomatic root are larger in bonobos relative to basicranial length.

Recent landmark-based GM studies have improved our understanding of the morphological relationship between the bonobo and chimpanzee within multivariate shape space, confirming earlier findings that they deviate from pure ontogenetic scaling. Williams et al. (2002) found that multivariate scaling only partially accounts for differences between bonobos and chimpanzees. In a GM study of facial landmarks, Cobb and O'Higgins (2004) found that, although the bonobo and chimpanzee appear to have a common ontogenetic shape trajectory compared to the gorilla, when PC1 and PC2 are plotted against each other (together, explaining 54% of the shape variation), the trajectories of other PCs are significantly divergent. In addition, Mitteroecker et al.'s (2004, 2005) analysis of the first three principal components of craniofacial landmarks among chimpanzees and bonobos confirmed that the two species follow different ontogenetic shape trajectories after birth for PCs other than PC1. In other words, some of the differences between bonobo and chimpanzee skulls appear to be a consequence of developmental changes other than heterochronic transformation, including heterotopy—the rotation or translocation of growth fields relative to one another that leads to divergent ontogenetic trajectories in shape space (Zelditch and Fink, 1996).

Although the GM analyses of Cobb and O'Higgins (2004) and Mitteroecker et al. (2004, 2005) revealed potential nonheterochronic differences in development between bonobos and chimpanzees, these studies did not test hypotheses of heterochronic transformation directly or explicitly, in part because they did not incorporate data on age. In addition, these studies did not test separately for regional heterochronies in the skulls, such as in the face and in the neurocranium, which comprise two different potential modules. This analysis therefore builds on previous studies by addressing the question of bonobo paedomorphosis using GM methods to measure multivariate shape and size both within the skull as a whole and within the two major modular units of the skull, the face and the neurobasicranial complex (NBC) (Lieberman et al., 2000a). In addition, we attempted to estimate relative age using dental-maturation criteria, allowing a full analysis of heterochrony.

Two major hypotheses are tested. Hypothesis 1 is that the bonobo skull as a whole is paedomorphic with respect to the chimpanzee. Hypothesis 2 is that any heterochronic transformations of the facial and neurocranial regions between these species are decoupled from one another, and that only part of the bonobo skull is paedomorphic with respect to the chimpanzee. For simplicity, both hypotheses assume that the bonobo is the descendant species, but we caution that this assumption is neither necessarily true nor testable given available data. As outlined in Klingenberg (1998) and Alba (2002), the two hypotheses are tested using data on the parameters of size, shape, and relative age (stage). Allometry is used to test for a common trajectory of size vs. shape, against which deviations from scaling can be determined.

¹ Shea's (1983a) analysis mistakenly reversed the labels for bonobos and chimpanzees in his Fig. 1C; when corrected, they lead to a diagnosis of peramorphosis (see Shea, 2000).

Materials and methods

Samples

This study used CT scans of 30 *Pan troglodytes* and 19 *Pan paniscus* skulls, which are listed in Table 1 by sex and dental stage. Although this reduces sample sizes, CT scans are used in order to include major landmarks of growth that are on the inside of the cranium and that cannot be measured from external landmarks (see below). Use of CT-scanned skulls also allows us to estimate age using crown and root development (see below). The chimpanzee skulls come primarily from a single population of Liberian chimpanzees from the collections of the Peabody Museum of Harvard University; these were supplemented by four juveniles from the A.H. Schultz collection (Anthropological Institute and Museum, University of Zurich, Switzerland). Chimpanzees from the Peabody Museum were scanned using a Siemens multiarray-detector scanner with a slice thickness of 0.5 mm (reformatted into isotropic voxels of 0.488 mm); chimpanzees from Zurich were scanned using a Siemens Somatom Sensation multislice CT scanner with a slice thickness of 0.5 mm, and serial cross sections reconstructed at 0.4-mm intervals. The bonobos are from the collection of the Musée de l'Afrique Centrale in Tervuren, Belgium. All but four were scanned by J. Braga using a Siemens Somatom Esprit Spiral CT (slice thickness typically varied among samples but ranged between 0.33 and 0.50). Four additional adult bonobos from Tervuren were included in the sample (29040, 29045, 23509, 26939); these individuals were scanned at the University Hospital, Leuven (Belgium), using a Siemens Somatom Sensation CT scanner with a slice thickness of 0.5 mm. Note that both samples comprised multiple individuals of both sexes from all stages of development—infant, juvenile, subadult, and adult—as assessed by dental stage (see below). One limitation of the sample is its modest size, which results from restricting the sample to CT-scanned crania. Restricting the analysis to scanned individuals is useful in order to incorporate internal landmarks that provide information on the location of key growth sites (such as in the cranial base) that are unavailable from external landmarking methods; in addition, the sample is large enough to estimate confidence limits for slopes and intercepts using standard statistical methods.

Aging

Age is the most challenging parameter to estimate for the samples used here, particularly for bonobos, for which there are almost no developmental data from known-age samples (for reviews, see Kinzey, 1984; Smith et al., 1994). Several challenges need to be considered in order to incorporate age estimates in this study. The most problematic issue is circularity of logic. Given the absence of aging studies on bonobos, it is necessary to use studies of chimpanzees and other apes to estimate bonobo ages. Although it is not possible to use comparative data to estimate the *chronological age* of the bonobos sampled here, several lines of evidence suggest that it is reasonable to use dental-maturation criteria from other African

Table 1
Sample used

Individual	Species	Dental age ¹	Sex
26938	<i>P. paniscus</i>	3.75	M
29021	<i>P. paniscus</i>	4.5	?
29022	<i>P. paniscus</i>	5.5	?
29029	<i>P. paniscus</i>	6.5	?
26990	<i>P. paniscus</i>	2.75	F
26979	<i>P. paniscus</i>	3.5	M
26958	<i>P. paniscus</i>	3.5	M
26992	<i>P. paniscus</i>	2.25	F
29008	<i>P. paniscus</i>	1.5	F
22336	<i>P. paniscus</i>	3.75	?
26977	<i>P. paniscus</i>	3.5	F
29061	<i>P. paniscus</i>	2.75	M
27010	<i>P. paniscus</i>	5.75	F
29066	<i>P. paniscus</i>	9	M
29052	<i>P. paniscus</i>	11+	?
29040	<i>P. paniscus</i>	11+	F
29045	<i>P. paniscus</i>	11+	F
23509	<i>P. paniscus</i>	10.5	M
26939	<i>P. paniscus</i>	11+	M
AM6892	<i>P. troglodytes</i>	3.25	F
AM7659	<i>P. troglodytes</i>	1.25	F
AM8606	<i>P. troglodytes</i>	2.5	M
AS1813	<i>P. troglodytes</i>	2.5	M
6918	<i>P. troglodytes</i>	10.5	F
7288	<i>P. troglodytes</i>	7.5	F
7286	<i>P. troglodytes</i>	10.5	F
6917	<i>P. troglodytes</i>	11+	M
7591	<i>P. troglodytes</i>	7.25	M
7562	<i>P. troglodytes</i>	11+	F
6915	<i>P. troglodytes</i>	11+	M
6913	<i>P. troglodytes</i>	11+	M
7296	<i>P. troglodytes</i>	5	M
7270	<i>P. troglodytes</i>	8.5	F
7266	<i>P. troglodytes</i>	2.5	F
7542	<i>P. troglodytes</i>	9	M
7566	<i>P. troglodytes</i>	11+	M
6923	<i>P. troglodytes</i>	11+	M
6929	<i>P. troglodytes</i>	8.5	M
7560	<i>P. troglodytes</i>	8.5	M
7545	<i>P. troglodytes</i>	11+	F
6953	<i>P. troglodytes</i>	11+	M
7280	<i>P. troglodytes</i>	3	F
7283	<i>P. troglodytes</i>	11+	M
6961	<i>P. troglodytes</i>	9	F
6949	<i>P. troglodytes</i>	11+	F
6970	<i>P. troglodytes</i>	11+	M
7262	<i>P. troglodytes</i>	6	M
7265	<i>P. troglodytes</i>	11+	F
7284	<i>P. troglodytes</i>	6.75	F

Individuals that had reached full dental maturity are listed as 11+.

¹ Relative age estimates based on Kuykendall (1996) and Dean and Wood (1981) (see text for details).

apes to estimate their *relative ontogenetic stage*, which is a useful variable to employ in heterochrony analyses (for review, see Smith, 2001). First, although the sequence of tooth eruption is notoriously variable within species, the general eruption sequences in bonobos and chimpanzees are essentially identical for both the permanent and deciduous dentitions (Boughner and Dean, 2004), with delay of the I2 being the most common difference (Kinzey, 1984). Second, estimates of the age of

eruption of deciduous teeth from a small sample of bonobos ($n = 4$) fall within the chimpanzee range, although at the low end (Smith et al., 1994). Finally, there is general similarity in the postnatal timing of tooth eruption and the relationship of these events to craniofacial maturation among the great apes. As Fig. 2 shows, the ages of eruption of the permanent teeth are not significantly different in captive male and female chimpanzees, and in a pooled sample of captive gorillas. Given these similarities, as well as those of various fossil apes (e.g., Beynon et al., 1998; Kelley and Smith, 2003), it is reasonable to assume that the sequence and relative timing of dental development in bonobos and chimps are sufficiently similar to compare them using the same criteria. Put differently, it would be surprising if the general sequence, pattern, and *relative* rate of eruption of the dentition in bonobos differed significantly from that of other African apes. Finally, even if the chronological rate of dental developmental differs between these species, the relationship between these events and craniofacial development appears to be broadly conserved among primates. Most importantly, M1 eruption occurs near the time of the cessation of neural growth, and M3 eruption occurs close to the completion of craniofacial growth (Schultz, 1960; Smith, 1989, 1991; Kelley and Smith, 2003).

A second problem to consider is that recent research (Zihlman et al., 2004) has confirmed that wild animals mature more slowly, but in the same sequence, than captive animals,

for which almost all aging data come (see Fig. 2). Therefore, more longitudinal data from wild populations of all ape species would be preferable in order to estimate their absolute ages. In actual fact, rate differences between wild and captive populations highlight the point made above that dental-aging estimates for all the species analyzed here must be treated as relative rather than absolute age estimates. Such estimates have their limitations but are nonetheless fully compatible with the logic of heterochrony analysis (Gould, 1977, Smith, 2001; German, 2004).

A third problem is that the only aging data available for the genus *Pan* come from cross-sectional studies (Dean and Wood, 1981; Kuykendall, 1996; Anemone et al., 1996), which yield more error than longitudinal studies. Longitudinal data from both species would be better (but present their own problems in terms of aligning individual trajectories), but as shown by German (2004), cross-sectional data are still useful despite their lower resolution when there is general similarity in terms of the slope of the relationship between ontogenetic events and time. For the time being, lack of longitudinal data limits the resolution of all studies of heterochrony in apes.

Accordingly, ontogenetic stage was estimated for both species using two studies: one by Dean and Wood (1981) and the other by Kuykendall (1996). First, CT images of each mandible were used to estimate age using tooth-developmental stages from Dean and Wood's (1981) study. Because Kuykendall

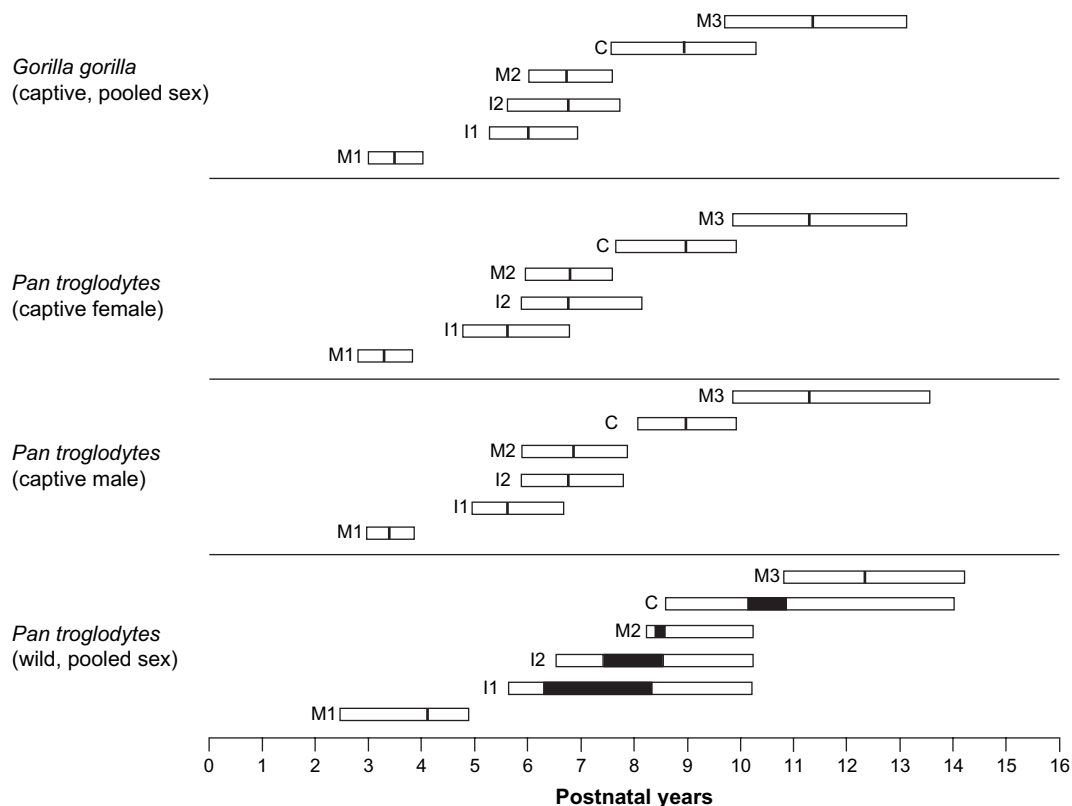


Fig. 2. Age of eruption of the permanent dentition of African apes, captive vs. wild, based on data from Smith et al. (1994) and Zihlman et al. (2004). Solid bars indicate means, including error ranges for mean estimates from Zihlman et al. (2004). Note that, although wild chimpanzees are shifted toward more delayed eruption times, the general pattern and sequence of eruption timings do not vary between species.

(1996) showed that only canines displayed sexual dimorphism in tooth eruption in *Pan*, canine maturation was not considered in the analysis. As a second step, estimates based on Dean and Wood's (1981) stages were then checked against age estimates derived using the tooth-formation stages for I_1 , M_1 , M_2 , and M_3 from Kuykendall's (1996) study. In all cases, the dental-age estimate derived using Dean and Wood's (1981) stages fell within the range derived from Kuykendall's (1996) stages. Note that the ontogenetic-age estimates used here are not estimates of absolute chronological age for either species. In other words, the heterochronic transformations that can be diagnosed in this analysis are limited to changes in the relative sequence of ontogenetic events, not absolute time.

Landmarks

Twenty-seven craniofacial landmarks, listed and defined in Table 2, were used. The landmarks were chosen to represent points from the neurocranium, face, and cranial base, and they include a number of internal sites of craniofacial growth. According to Bookstein's (1991) categorization, 30% are type I landmarks (points where three structures meet or sites of locally unusual histology); 60% are type II landmarks (points whose homology is supported by geometric criteria, such as tooth tip or maxima of curvature); and only 10% are type III landmarks (extremal points whose definitions refer to information from diverse, finitely separated locations such as end-points). After rendering the skulls using VG StudioMax Pro[®], each landmark was expressed as a point in 3D space using Cartesian coordinates. To assure correct placement, all landmarks were taken by examining the location of the point (indicated visually by cross-hairs) on both the rendered cranium and in three orthogonal planes (sagittal, coronal, and transverse). In the rare case of a missing landmark due to specimen damage, the landmark was estimated as accurately as possible using visual means from the surrounding skeletal tissue.

Landmark precision and accuracy were both evaluated. Precision was evaluated by taking all 27 craniofacial landmarks from one chimpanzee (#6918) on five separate occasions. Two-tailed paired Student's *t*-tests between pairs of landmark-coordinate sets found no significant differences ($p > 0.61$). The average standard deviation of landmark coordinates in the *x*, *y*, and *z* planes was between 0.50 and 0.57 mm, indicating that landmark locations can be determined consistently and with an acceptable degree of error. Accuracy was evaluated by comparing interlandmark distances obtained through VG StudioMax Pro[®] with distances obtained using electronic calipers on the same cranium. Nine interlandmark distances were used: nasion–rhinion, bregma–lambda, zygomaxillary orbitale–zygofrontal orbitale, basion–incisive canal, basion–palatal intersection point, nasion–metopion, upper orbital rim–zygomaxillary orbitale, jugale–C–I2 alveolar ridge, and basion–zygomaxillare. A two-tailed paired *t*-test of the distance values found no significant difference ($p = 0.87$) between these two sets with an average interlandmark difference of 0.52 mm.

Geometric morphometrics

Morphologika[®] software Version 2.0 (www.york.ac.uk/res/fme/resources/software.htm) was used to translate, rotate, and then scale via a generalized least squares (GLS) superimposition the landmark configurations for all individuals; the program was then used to calculate and graph the principal components of shape variation using the variance-covariance matrix of the resulting Procrustes residuals (O'Higgins, 2000). Size was calculated as centroid size (i.e., the square root of the sum of the squared deviations of landmarks from a centroid point). These analyses were performed not only on the skull as a whole, but also separately on subsets of landmark points from the face using landmarks 1–15 and from the NBC (neurocranium and basicranium) using landmarks 16–27. Shape changes in the skull were visualized using a wireframe connecting adjoining landmarks (Fig. 3).

Best-fit reduced major axis (RMA) regression lines for chimpanzees and bonobos were calculated, and differences in the slopes and intercepts were tested using ANCOVA (calculated from least square regressions) with an alpha level of 0.05 to indicate significance. In order to avoid assuming linearity, significance was also evaluated using ANOVA comparisons of the two species divided into four age categories: I, up to 3 years; II, from 3 to 6 years; III, from 6 to 9 years; IV, greater than 9 years. To facilitate interpretation of the bivariate scattergrams, individuals in Figs. 4–7 are differentiated by sex and the four age categories.

Results

Principal components of shape variation

Analysis of all 27 cranial landmarks resulted in 42 nonzero eigenvectors, whose eigenvalues indicate a pattern of shape variation that is primarily quantified by PC1 (71.7%) (Table 3). Permutations of the analysis that alter the number of variables and individuals result in little change to the shape space (data not shown). Figure 4A, which plots the first two PCs, indicates that PC1 discriminates to some extent between the two species, but with overlap. The bonobo and chimpanzee samples create clouds that reflect trajectories of development from negative to positive PC1 scores (left to right). When adult males are removed from the analysis, an ANCOVA finds no significant difference in the slope of PC1 vs. PC2 for either species. Wireframes of the shape space quantified by the PCs indicate that each component quantifies an integrated suite of features that reflects several coordinated ontogenetic changes that have also been documented in other analyses of ape ontogeny (Mitteroecker et al., 2004, 2005; Cobb and O'Higgins, 2004; Guy et al., 2005). Low values for PC1 represent individuals with smaller, shorter palates; shorter faces that are more ventrally rotated under the cranial vault; rounder and relatively larger cranial vaults; and more flexed cranial bases. Individuals with more positive PC1 values have relatively larger and more prognathic faces that are more dorsally rotated, have a relatively smaller and more oval-shaped

Table 2
Landmarks used

Landmark	Type ¹	Region	Definition
1 Nasion	I	Face	Midline intersection of nasal and frontal bones
2 Glabella	II	Face	Most anterior midline point on the frontal bone at the level of the supraorbital torus
3 Rhinion	II	Face	Midline point at the inferior end of the internasal suture
4 Anterior nasal spine	II	Face	Most anterior and posterior point on nasal spine
5 Incisive canal	II	Face	Most anterior and inferior midline point of incisive canal on the hard palate
6 Palatal intersection point	I	Face	Midline intersection of palatal and palatine sutures
7 Zygomaxillary-orbitale	I/II	Face	Point where zygomaxillary suture intersects orbital margin
8 Uppermost orbital rim	II	Face	Most superior point on the orbital margin
9 Ectochochion-zygofrontal	I/II	Face	Point where zygofrontal suture intersects orbital margin
10 Zygomaxillare	I/II	Face	Most inferior and lateral point on the zygomaxillary suture
11 Alare	II	Face	Most lateral point on the margin of the nasal aperture
12 Maxillary tuberosity	II	Face	Most posterior point of the alveolar crest below the palatine suture
13 M1-M2 alveolar margin	II	Face	Point at center of alveolar crest between M ¹ and M ²
14 C-I2 alveolar margin	II	Face	Point at center of alveolar crest between I ² and the canine
15 Jugale	II	Face	Deepest point of notch between the temporal and frontal processes of the zygomatic
16 Basion	II	NBC ²	Most anterior and inferior midline point on the margin of the foramen magnum
17 Sella	III	NBC	Point (in space) at the center of the sella turcica
18 Foramen caecum	I	NBC	Most anterior inferior point of anterior cranial base
19 Sphenoidale	II	NBC	Most superior and posterior midline point on the tuberculum sellae
20 Posterior cribriform plate	II	NBC	Most posterior and inferior point on surface of cribriform plate
21 Spheno-occipital synchondrosis	II	NBC	Exterior midline point on the suture between the sphenoid and occipital
22 Parietopion	III	NBC	Midline ectocranial point at the greatest elevation above the chord from bregma to lambda
23 Opisthion	II	NBC	Midline point at posterior margin of the foramen magnum
24 Opisthocranium	III	NBC	Midline ectocranial point at the farthest chord length from the glabella
25 Lambda	I	NBC	Ectocranial midline point of actual or projected intersection of sagittal and lambdoidal sutures
26 Bregma	I	NBC	Ectocranial midline point at intersection of coronal and sagittal sutures
27 Metopion	III	NBC	Ectocranial midline point on frontal at its greatest elevation relative to the chord from nasion to bregma

¹ Types correspond to categories of Bookstein (1991).

² NBC, neurobasicranial complex (see Lieberman et al., 2000a).

neurocranium, and more extended cranial bases. The second PC, which accounts for only 5.5% of the variation, primarily separates individuals with higher versus lower cranial vaults, particularly above the orbits.

Plots of the first two principal components in analyses of just the facial landmarks (1–15) and just the NBC landmarks (16–27) reveal interesting differences, with much less variance explained by the first principal component. In the facial analysis (Fig. 4B), the first PC accounts for only 36.4% of the total variation, but discriminates the two species at all but the earliest ontogenetic stage. With adults removed, the slopes of the ontogenetic trajectories differ significantly for the two species (ANCOVA, $p < 0.05$). Individuals with higher PC1 scores are more prognathic, have a longer rostrum, particularly in the posterior portion of the face, and have relatively smaller orbits. The second PC (12.1%) primarily describes variations in palate angle and facial width. In the NBC landmark analysis (Fig. 4C), the PC1 axis discriminates the two species but with ontogenetically staggered overlap and no significant difference in slope between the two species. Bonobos generally have lower PC1 values than chimps of the same relative ontogenetic stage. The first PC in this analysis explains 56.7% of the variance (Table 3). As is evident from Fig. 4C, individuals with lower PC1 scores have more flexed cranial bases, with more globular braincases, more anteriorly positioned foramina magna, and relatively shorter anterior cranial bases. The second PC explains relatively less variation,

primarily in terms of the relative height of landmarks at the posterior end of the cranial vault (many of which are type III landmarks). As in the face, the PC1 axis primarily discriminates bonobos and chimpanzees, with bonobos and

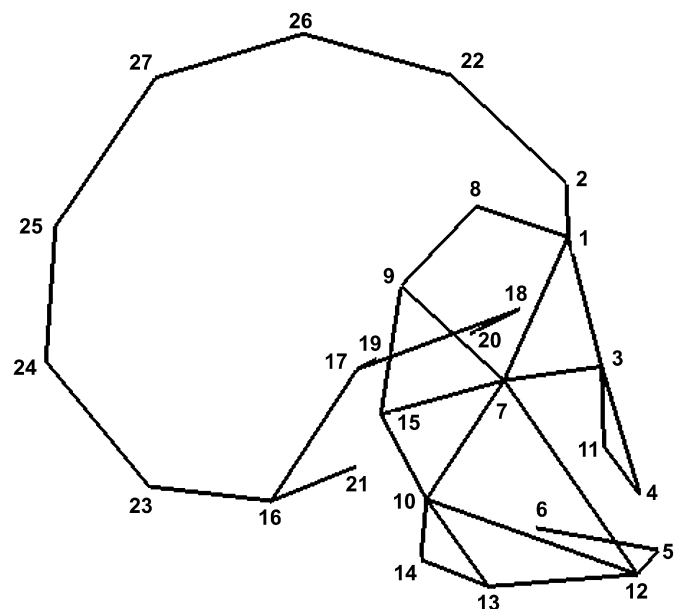


Fig. 3. Landmarks used in the analyses (numbers correspond to definitions in Table 2).

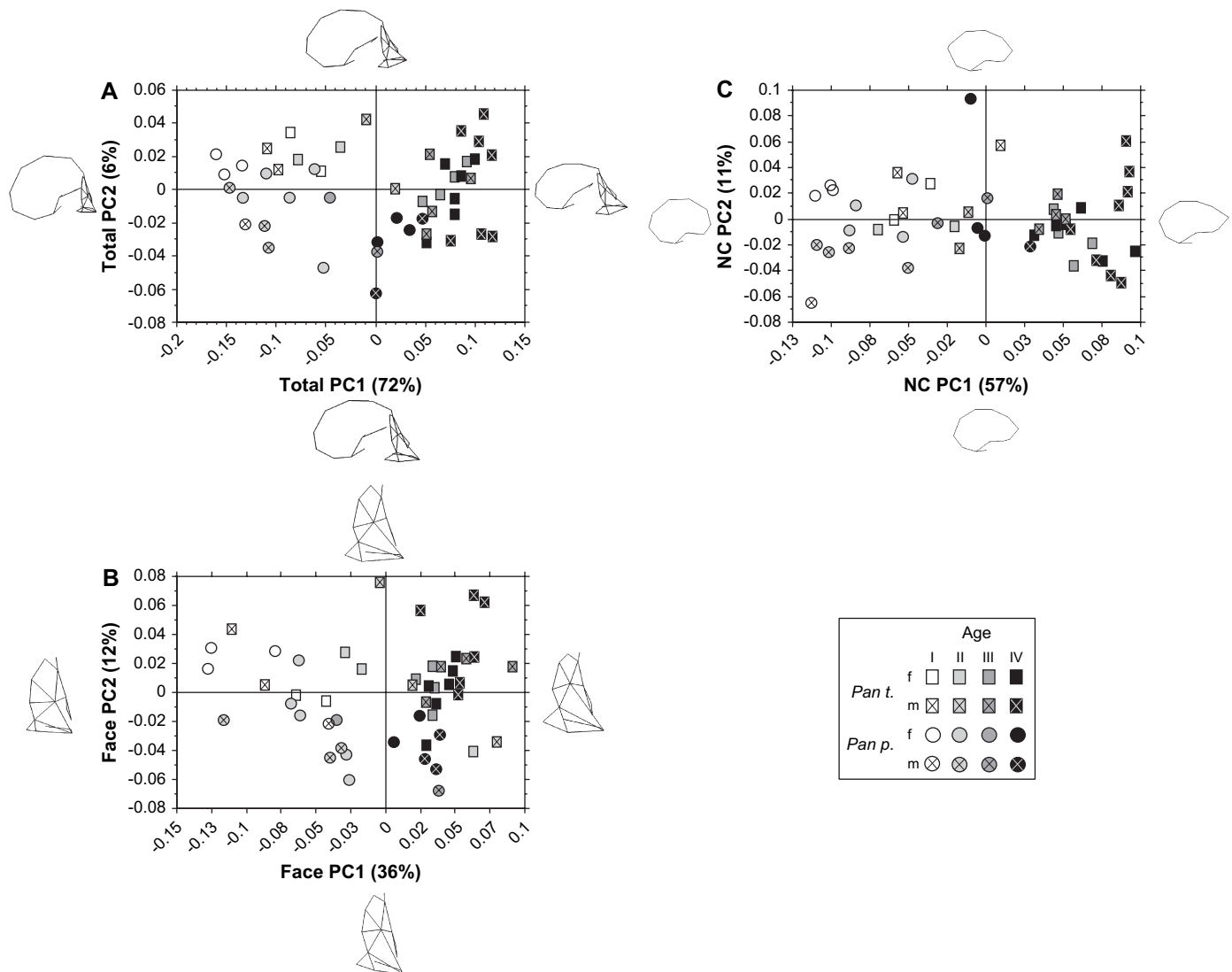


Fig. 4. Plots of PC1 vs. PC2 for analyses of the entire cranium (A), face (B), and neurocranium and basicranium (C). Wireframes indicate extreme landmark configurations for each principal component.

chimpanzees generally occupying respectively smaller and larger PC1 values. On this axis, adult bonobos lie in the same shape space as young chimpanzees. The second PC does little to discriminate individuals by sex, age, or species in the facial and NBC analyses.

Heterochrony and allometry

Rates of shape change in both species were quantified by graphing PCs for each landmark set against age estimates, and ontogenetic allometries were quantified using centroid size against PCs (which were previously calculated from size-normalized data as described above). Because significant correlations ($p < 0.05$) were only found between PC1 and either relative age or size, we focus solely on PC1 of each analysis. Figure 5 and Tables 4 and 5 summarize the results for the entire cranium. When graphed in terms of heterochrony (Fig. 5A) both species have parallel shape trajectories with significantly different intercepts but not significantly different

slopes. Thus, for any given relative age, the bonobos are underdeveloped relative to chimpanzees, but fall along the same shape trajectory. These differences are confirmed by the ANOVA results (Table 5), which indicate that PC1 scores by age category are different at or near conventional levels of significance for all age categories, despite small sample sizes and the crudeness of the age categories themselves. However, the ontogenetic allometry (Fig. 5B) indicates that both species do not differ significantly in either slope or intercept when PC1 is plotted against centroid size. In combination, these results diagnose bonobos as paedomorphic relative to chimps via postformation, or initial underdevelopment for just this component of shape (i.e., just PC1). Note that the adult bonobos (male and female) fall in the shape space of the subadult chimpanzees for PC1.

Figure 6 plots analyses of just the facial landmarks. In terms of relative age versus shape (Fig. 6A), the intercept but not the slope of the RMA regression between PC1 of facial shape and dental age is significantly different (see Table 4)

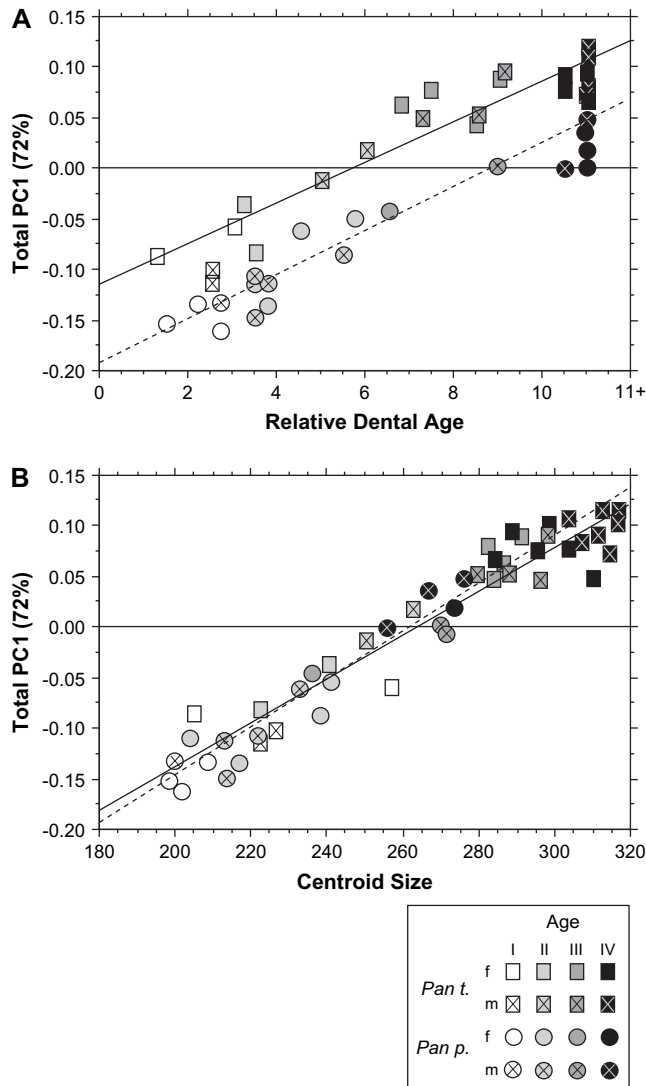


Fig. 5. PC1 vs. dental age (A) and centroid size (B) for entire landmark set.

between the two species. The same is also true, but to a lesser extent, of the ontogenetic allometry (Fig. 6B), and there is a general trend for bonobos of the same general stage to have smaller values for PC1 at all stages except the first (Table 5). As in the entire cranial analysis, the shape of the face for the largest adult bonobos falls in the shape space of subadult chimpanzee faces for PC1. To some extent, these results diagnose bonobo faces as pedomorphic relative to chimpanzees via postformation for just PC1, but much less strongly than in the analysis of the entire cranium. Therefore, one cannot conclude that the bonobo face is predominantly different from chimpanzees via pedomorphosis because PC1 explains less than 40% of the total variance of this particular sample. As always, larger samples of adult bonobos and juvenile chimps and more landmarks will help to clarify these results.

Finally, Fig. 7 and Tables 4 and 5 summarize results from analyses of just the landmarks from the neurocranium and basicranium (NBC). These analyses generally resemble those for the entire cranium, with significantly different intercepts but not slopes for PC1 vs. dental age, and no significant difference

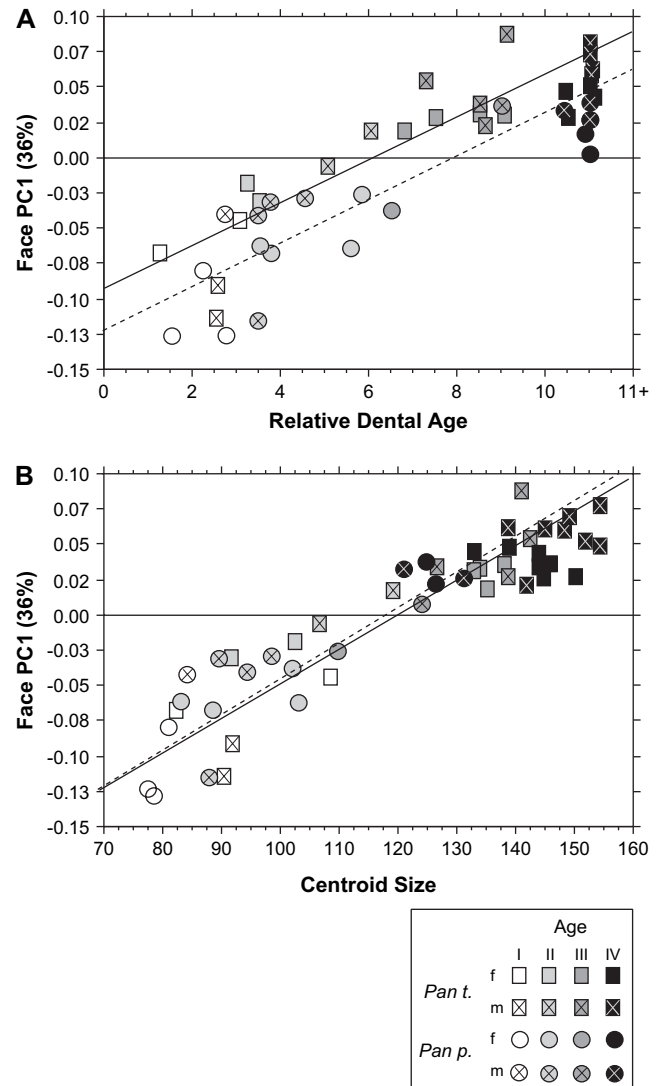


Fig. 6. PC1 vs. dental age (A) and centroid size (B) for facial landmark set.

in slope or intercept for PC1 vs. centroid size. As was the case with respect to the whole cranium, the bonobo NBC appears to be pedomorphic via postformation, with adult bonobos falling in the shape space of subadult juvenile chimpanzees for PC1 (56.7% of the variance) and no statistically significant difference in ontogenetic shape trajectory.

Discussion

Overall, the results presented here lend support to the hypothesis that the bonobo cranium differs partially but not entirely from the chimpanzee cranium because of pedomorphosis. In particular, results for the entire cranium indicate pedomorphosis via postformation (initial shape underdevelopment) for just the first principal component of variation because analyses of PC1 versus estimates of relative age indicate similar slopes but with a higher intercept for the chimpanzee sample. In addition, the ontogenetic allometries of the two species for PC1 are the same in terms of slope and intercept, but with adult bonobos falling in the shape space of subadult

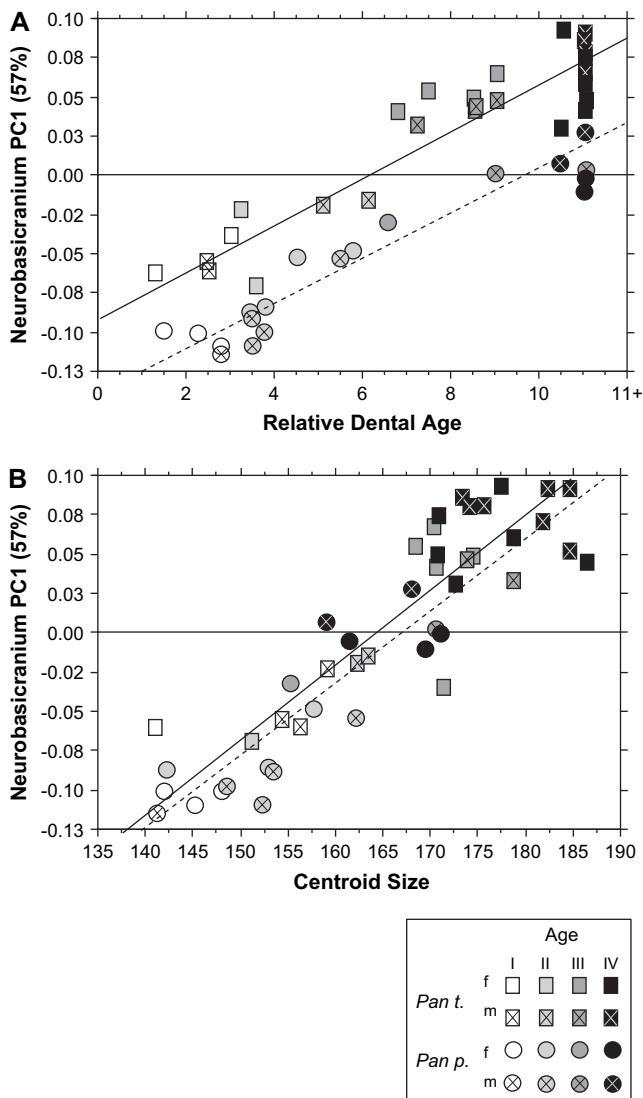


Fig. 7. PC1 vs. dental age (A) and centroid size (B) for neural and basicranial landmark set.

chimpanzees. Thus, bonobo and chimp cranial growth follow the same ontogenetic allometric trajectory for PC1, but for any given age, bonobo crania are underdeveloped relative to those of chimpanzees. These results generally support previous hypotheses of paedomorphosis for bonobos (e.g., Shea, 1983a, b, 1984, 1985; Alba, 2002; Ponce de León and Zollikofer, 2006), but differ slightly in the type of paedomorphosis diagnosed, and in the extent to which paedomorphosis is responsible for the species' contrasts.

As noted by other authors (e.g., Mitteroecker et al., 2005), it can be problematic to analyze the entire cranium as a whole. Importantly, the above results offer limited support for the second hypothesis that heterochronic transformations of the facial and neurocranial regions are partly dissociated from one another and thus contribute differently to paedomorphosis of the cranium as a whole. As noted above, the results for the NBC generally resemble those of the entire cranium, suggesting paedomorphosis via postformation, but the analysis of

Table 3

PCA variance components (>5%) for whole skull, face, and vault

	Cranium	Face	Neurobasicranium
PC1	71.7	36.4	56.7
PC2	5.5	12.1	10.9
PC3	—	10.2	5.6
PC4	—	7.2	—
PC5	—	5.0	—

only facial landmarks indicates significant differences in the intercept between age vs. PC1 and size vs. PC1. In other words, the face does not appear to be paedomorphic in the same pattern and to the same extent as the NBC or the entire cranium. Recall also that PC1 in the facial analysis only explains 38% of the total variance in this sample. This calculation does not mean that the bonobo face is precisely 38% paedomorphic because the exact proportion of variance explained by any given component is a function of many factors, including the size and nature of the sample, as well as the landmarks used. Further analyses with larger samples and better age data will help clarify the results reported here, but it is reasonable to conclude that other developmental differences such as heterotopy are likely to explain a large if not dominant proportion of the facial differences between these samples. Interestingly, similar results were obtained by Cobb and O'Higgins (2004) for just facial landmarks using a larger sample of hominoid species. Other researchers have also shown that the face is more paedomorphic relative to the NBC in bonobos compared to chimpanzees (Cramer, 1977; McHenry and Corruccini, 1981; Shea 1983a; Alba, 2002).

Regardless of what patterns of paedomorphosis explain the variation quantified by PC1, the results of this analysis also support the hypothesis that the bonobo skull is only partially paedomorphic with respect to the chimpanzee. More precisely, the bonobo is partially paedomorphic relative to the chimpanzee, more so in the vault and cranial base, and less so in the face. However, as discussed above, a problematic issue is determining what percentage of variation can be explained by paedomorphosis or any other pattern of heterochrony. Mitteroecker and colleagues (2005) argued that one cannot diagnose heterochrony using GM or other multivariate analyses if the first few principal components of variation do not follow identical ontogenetic trajectories. However, one advantage of using GM methods to quantify shape variation is that they identify combinations of variables that covary independently and that scale with size and age. Thus, the methods employed here are able to detect without a priori models what aspects of the bonobo cranium are heterochronic transformations of the chimpanzee cranium (or vice versa). Such diagnoses still need to be interpreted biologically using developmental data from other kinds of analyses. In fact, these diagnoses are primarily useful for generating hypotheses about developmental shifts (Lieberman et al., 2004).

Another way to consider this issue is via a thought experiment. If one agrees that evolutionary change can occur through multiple mechanisms including (but not exclusively) heterochrony, then how would one set about to generate and

Table 4
Reduced major axis regression results¹

	Bonobo (<i>n</i> = 19)			Chimpanzee (<i>n</i> = 30)			ANCOVA	
	Intercept (±s.d.)	Slope (±s.d.)	<i>r</i>	Intercept (±s.d.)	Slope (±s.d.)	<i>r</i>	Slope	Intercept
Entire cranium								
CS vs. PC1	−0.657 (0.04)	0.003 (0.003)	0.966	−0.568 (0.04)	0.002 (0.0003)	0.887	NS	NS
Age vs. PC1	−0.190 (0.08)	0.020 (0.003)	0.963	−0.127 (0.01)	0.013 (0.002)	0.869	NS	*
Facial landmarks								
CS vs. PC1	−0.487 (0.05)	0.002 (0.001)	0.867	−0.273 (0.03)	0.002 (0.001)	0.895	NS	*
Age vs. PC1	−0.128 (0.05)	0.015 (0.004)	0.874	−0.097 (0.01)	0.015 (0.003)	0.869	NS	*
Neurobasicranial landmarks								
CS vs. PC1	−0.809 (0.05)	0.005 (0.001)	0.878	−0.778 (0.09)	0.005 (0.002)	0.829	NS	NS
Age vs. PC1	−0.137 (0.04)	0.014 (0.002)	0.953	−0.092 (0.02)	0.015 (0.002)	0.933	NS	*

¹ Abbreviations are as follows: CS, centroid size; NS, not significant; **p* < 0.05.

test hypotheses about what developmental shifts actually occurred in a particular evolutionary transformation? Until recently, researchers primarily addressed such questions using a typical hypothetico-deductive method, taking measurements of cross-sectional samples of two or more species, and analyzing the slope and intercept of various combinations of the parameters. Variables that scaled significantly with size were then analyzed further using various heterochrony models, whereas variables uncorrelated with size were discounted from further analysis. Such studies therefore incorporated the assumption (often implicit) that not all transformations between ancestral and descendant species are captured by allometry and heterochrony. However, the methods they used offered few means of quantifying how much of the total variation between the species was related to scaling, and for diagnosing other mechanisms that could cause nonallometric changes. Therefore, the logic used by Mitteroecker et al. (2005) applies no less to all kinds of heterochrony analyses; it is simply more obvious from GM analysis (a point they acknowledged). As they noted, GM methods offer advantages unavailable to simple univariate approaches because they provide estimates (albeit context-dependent) of the percentage of variation that particular transformations cause, they can help generate hypotheses about the biological mechanisms that might account for these transformations, and they may also diagnose alternative mechanisms to be explored.

Viewed in this light, the results reported here confirm those of other GM analyses relating to this problem. Heterochrony alone is an insufficient framework to interpret whatever evolutionary changes occurred to make bonobos and chimpanzees different from one another. In this analysis, PC1 accounts for a strikingly limited proportion (<50%) of variation in

the face, and the first PCs of the entire cranial and NBC analyses do not account for 25% and 33% of the variation, respectively. These data thus support the conclusions of other GM analyses (Cobb and O'Higgins, 2004; Mitteroecker et al., 2004, 2005; Ponce de León and Zollikofer, 2006) that scaling alone cannot explain all of the differences in cranial shape between bonobos and chimpanzees. Instead, future research using different analytical methods and additional data should focus on potential nonheterochronic contributions to the differences evident between the species. This conclusion is evident from differences in the ontogenetic trajectories between the species, and from the fact that other PCs that explain significant amounts of variance have no obvious or significant correlation with sex or age for these analyses (e.g., PC2 in Fig. 4). A related caveat to consider is that correlations in shape change expressed by principal components only quantify changes in the configuration of the landmarks included in the analysis. It follows that the biological processes that underlie these changes may not be adequately represented by any one principal component, and/or a single principal component may correspond to more than one covarying process of change (Tissot, 1988). Ultimately, the shape changes these principal components describe need to be related to particular developmental processes.

Finally, while some proportion of the differences between bonobo and chimpanzee crania apparently derive from pedomorphosis, additional data are needed to test more securely the diagnosis of pedomorphosis via postformation. Most crucially, we need new methods to age individuals without reference to cross-sectional samples of captive populations. However, it is reasonable to hypothesize that larger and better-aged samples will confirm the above results given the

Table 5
ANOVA results for relative dental age vs. PC 1 (standard error in parentheses)

Age	Total cranium (PC1)			Face (PC1)			Neurobasicranium (PC1)		
	Chimpanzee	Bonobo	<i>p</i>	Chimpanzee	Bonobo	<i>p</i>	Chimpanzee	Bonobo	<i>p</i>
0–3.0	0.09 (0.01)	0.15 (0.01)	0.06	−0.08 (0.02)	−0.09 (0.02)	NS	−0.05 (0.01)	−0.11 (0.00)	0.003
3.1–6.0	0.03 (0.02)	0.10 (0.01)	0.07	−0.01 (0.01)	−0.06 (0.01)	0.02	−0.03 (0.01)	−0.08 (0.01)	0.009
6.1–9.0	−0.06 (0.01)	0.02 (0.01)	<0.001	0.04 (0.01)	0.00 (0.01)	0.08	0.05 (0.00)	−0.02 (0.1)	<0.001
>9.0	−0.09 (0.00)	−0.02 (0.01)	<0.001	0.05 (0.00)	0.02 (0.01)	0.07	0.07 (0.00)	0.00 (0.01)	0.001

findings of previous analyses using external landmarks and/or measurements from much larger samples (e.g., Shea, 1983a, 1984). Regardless of these caveats, bonobos evidently not only end their ontogeny at a smaller size and more juvenile shape than chimpanzees, but they also begin postnatal development at smaller sizes and more juvenile shapes. Indeed, bonobos at birth are approximately 0.5 kg lighter than chimpanzees (Smith and Leigh, 1998). Developmental differences between these two species thus appear to be present before birth, presumably as the result of regulatory shifts in fetal or embryonic development. It is interesting to speculate that such mechanisms—perhaps differences in circulating hormone levels or hormone receptor binding activities—may link the correlated suite of shifts evident in postcranial anatomy, the brain, or other organs that play some role in the behavioral differences between the species (Shea, 1983a, 1984, 1989; Blount, 1990). Testing these hypotheses is of importance not only for understanding how and why bonobos and chimpanzees differ, but also for understanding better how patterns of developmental differences in the phenotype can help identify candidate mechanisms and even the genes responsible for evolutionary developmental differences between closely related species.

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